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The Food and Feeding of *Trisopterus esmarkii* (Nilsson) in the Northern North Sea

By D. F. S. RAITT, B.Sc. and J. A. ADAMS, B.Sc.
Marine Laboratory, Aberdeen

November, 1964

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CONTENTS

	Page
Introduction	3
Material and Methods	3
The Food of *Trisopterus esmarkii*	5
Previous investigations	5
Present investigations	5
Variations in Feeding	19
Seasonal	19
Diurnal	19
Relations between the Food of *T. esmarkii* and the Zooplankton	21
The Food and Feeding of *T. esmarkii* Compared with O-Group Haddock and Whiting	23
T. esmarkii as a Food Species of Other Fish	26
A Summary of the Position and Importance of *T. esmarkii* in the Food Cycles of the Northern North Sea	27
Summary	27
References	28

The Food and Feeding of *Trisopterus esmarkii* (Nilsson) in the Northern North Sea

INTRODUCTION

As part of a programme of research into the life history and general biology of the Norway pout *Trisopterus esmarkii* (Nilsson) [formerly *Gadus esmarkii* Nilsson—for details of synonymy see Svetovidov, 1948], now being carried out at the Marine Laboratory, Aberdeen, a study has been made of its food and feeding habits. Preliminary reports of this work have already been given by Raitt (1961), and Raitt and Adams (1962). The present paper brings together the results described in these preliminary reports, but also presents a considerable amount of additional information.

The authors wish to thank Dr J. H. Fraser, Mr B. B. Parrish, Dr C. E. Lucas and the Editors for their help in the preparation of this paper.

MATERIAL AND METHODS

The samples were collected mainly during research vessel trawling surveys in the northern North Sea from 1960 to 1962, although one set of stomachs came from a Swedish trawler fishing on the Fladen in August 1960. Table I shows the various periods of sampling and the numbers of stomachs examined.

Two size-groups of *T. esmarkii* have been distinguished; 1) juvenile O-group fish, 8–13 cm long, and 2) 1 to 3-years-old maturing and adult fish of 14–21 cm. Although in some respects arbitrary, these two categories will be referred to hereafter, for convenience, as juveniles and adults. From May to August, no O-group fish were sampled, so that only the larger group is represented then; thereafter, the new year-class appears in the samples for the first time.

Wherever possible during each survey, stomachs were collected from 5 to 15 fish in each size category at each trawling position. These stomachs were preserved in 4% buffered formalin for subsequent analysis in the laboratory. For each trawling position the number of stomachs which were empty was noted, and the contents of the remainder were combined and analysed separately for each size-group.

Two types of analyses were carried out. For all surveys the volumes of the different food-types (e.g. copepods, euphausiids, fish, etc.) were measured by water displacement, while for a number of selected surveys (March–April 1961, March 1962 and November 1962) detailed specific analyses and counts were also made.

Comparisons were also made of the stomach contents of *T. esmarkii* with zooplankton samples taken in oblique hauls from near bottom to surface at each trawl position during March–April 1961, March 1962 and November 1962. The Gulf III plankton sampler used was the modified form with an 8 inch (20·3 cm) aperture (see Bridger, 1958; Gehringer, 1962; Southward, 1962). The mesh had a mean aperture of 0·23 mm. A Currie-Foxton depth flow-meter (Currie and Foxton, 1957) was placed in the tail cone.

On several of the surveys, stomachs were collected from O-group whiting, *Merlangius merlangus* (L.), and haddock, *Melanogrammus aeglefinus* (L.) less than 20 cm in length caught in the same hauls as the *T. esmarkii*. These stomachs were analysed to determine to what extent, if at all, they contained the same food species as *T. esmarkii*.

TABLE I

DATES OF SAMPLING AND NUMBERS OF STOMACHS EXAMINED

Numbers of empty stomachs in brackets

Period of Sampling		Stomachs examined			
		T Juveniles	T Adults	W	H
Explorer	6th–15th April 1960	56 (3)	98 (39)	—	—
Scotia	22nd May–1st June 1960	—	44 (2)	—	—
Zeron	16th August 1960	—	27 (16)	—	—
Scotia	11th–28th Sept. 1960	102 (17)	206 (27)	74 (7)	30 (0)
Scotia	18th February 1961	10 (1)	10 (0)	—	—
Scotia	13th Mar.–15th April 1961	62 (7)	198 (43)	37 (9)	14 (1)
Scotia	6th–22nd August 1961	—	45 (7)	32 (6)	10 (1)
Scotia	27th January 1962	—	10 (4)	—	—
Scotia	4th–19th March 1962	69 (17)	62 (21)	—	—
Explorer	30th May 1962	—	6 (0)	—	—
Scotia	12th–26th Nov. 1962	27 (0)	97 (20)	68 (28)	116 (6)
Totals		326 (45)	803 (179)	211 (50)	170 (8)

T — *Trisopterus esmarkii*
W — *Merlangius merlangus* (L.) (O-group)
H — *Melanogrammus aeglefinus* (L.) (O-group)

THE FOOD OF *TRISOPTERUS ESMARKII*

Previous Investigations

The first reference to the food of *T. esmarkii* known to the authors is that of Fries *et al.* (1892–5) who quote Collett as often finding in the stomachs of fish from the Christiania fjord "nothing but White Gobies (*Aphya minutus*), which seem to be the chief food of *Gadus esmarkii*".

Scott (1902, 1903), who examined a large number of *T. esmarkii* from the Moray Firth, North Sea and Firth of Clyde, recorded the stomach contents as consisting mainly of small crustaceans "but schizopods, *Parathemisto* and pelagic copepods were more frequently observed than other members of that group". He noted the predominance of pelagic species in the food.

Saemundsson (1929, 1949), referring to *T. esmarkii* in Icelandic waters, also found that their diet consisted mainly of small crustaceans. The principal species were *Calanus*, *Rhoda* (i.e. *Thysanoessa*) and *Meganyctiphanes*, but small scopelids were also recorded.

More recent work by Gokhale (1953) at the Isle of Man verified the importance of pelagic crustaceans in the diet of *T. esmarkii* from those waters. He summarizes his results as follows:

Food type	Percentage by volume of total food
Calanus finmarchicus / *Pseudocalanus elongatus*	33·9
Meganyctiphanes norvegica	27·0
Decapod larvae	12·2
Sagitta sp.	10·0
Pasiphaea sivado	6·8
Fish larvae	3·0
Nyctiphanes couchii	2·5
Other remains (including unidentified Crustacea)	4·6
	100·0

Total percentage Crustacea = 85·8%

Finally Gokhale observed that the older fish appeared to take more fish larvae.

Present Investigations

The food found in fish stomachs, at any one time, will not give an absolute estimate of the true quantity and proportion of the food species eaten, for it is obvious that some food species will be more easily and quickly digested than others, and therefore may be underestimated relative to other food forms. Such species will also be more difficult to recognise. An analysis of stomach contents, however, is often the only convenient method of estimating either the food eaten or the food assimilated.

It is also important to present the results in such a way as to give as representative and as unbiased a picture as possible. In comparing the importance of the food types of juvenile and adult *T. esmarkii*, the example of McIntyre (1953) has been followed. The data from the cruises during which both categories occurred (except February 1961, when only percentage feeding data are available) are initially shown in three different ways. Firstly, the number of stomachs containing each food-group is expressed as a percentage of the total stomachs containing food; this is the percentage occurrence. Secondly, the total volume of each food group is expressed as a percentage of the total volume of all food. Thirdly, the average volume per stomach, based on those stomachs containing the food group in question, is recorded. The presentation of the data in this form gives a more comprehensive picture than would otherwise be possible.

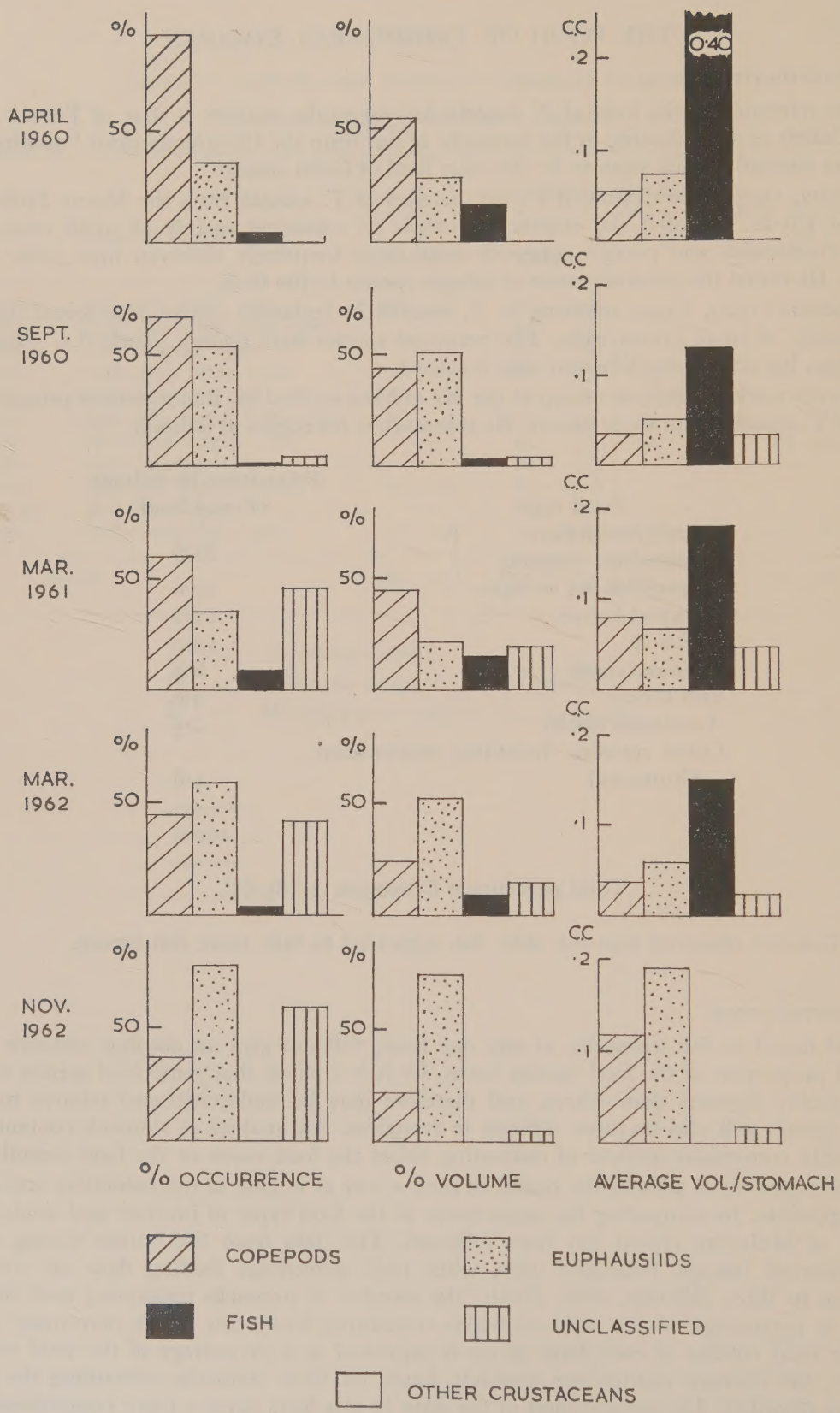

Fig. 1. Percentage occurrence, percentage volume and average volume per stomach of the main food types in the stomachs of *T. esmarkii* (Juveniles).

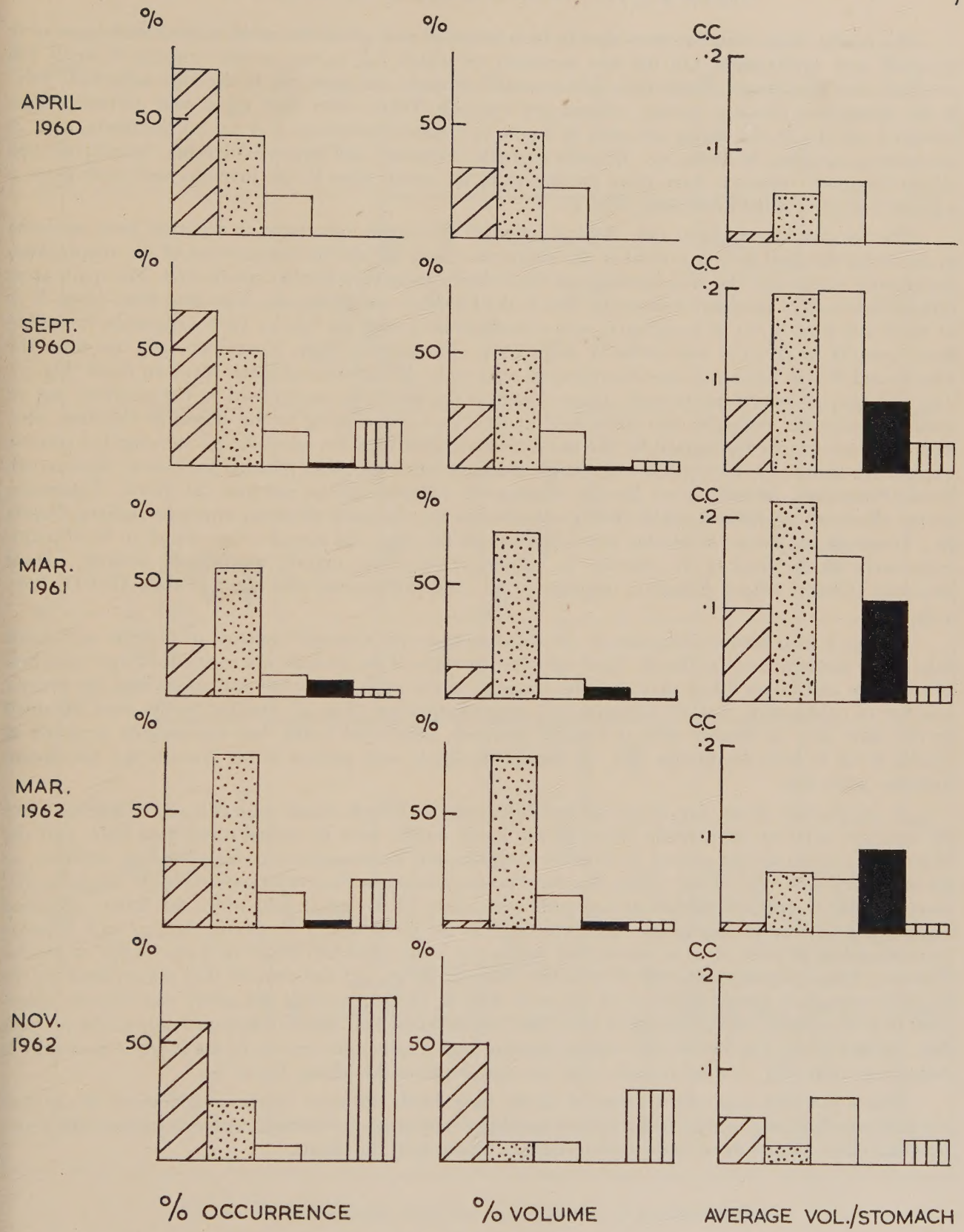

Fig. 2. Percentage occurrence, percentage volume and average volume per stomach of the main food types in the stomachs of *T. esmarkii* (Adults). (For key see Fig. 1.)

The results (Figs. 1 and 2) show that in both juveniles and adults the predominant food types were copepods and euphausiids. On the few occasions on which fish larvae or the remains of small fish occurred they constituted almost the entire stomach contents and gave rise to the high values of "fish" in the histograms showing average volume per stomach. When other food types were recorded these consisted mainly, in the spring samples, of *Sagitta* sp., appendicularians and natant decapods, and, in the autumn samples, of *Sagitta* sp., *Spiratella retroversa* (Fleming) and appendicularians. Amphipods and natant decapods, however, were more prominent in the adults than in the juveniles and were given a separate category in the histograms (Fig. 2).

The data for March–April 1961, March 1962 and November 1962 have, in addition, been analysed in detail for the food species present in the stomachs. Since the species composition of the zooplankton community varies over the area investigated these results have been further subdivided. The main areas differentiated are a northern area to the east of the Orkneys and Shetlands, extending from 58°30′N to 61°00′N and from 01°00′W to 03°00′E, and a southern area from the Moray Firth eastwards, extending from 57°00′N to 58°30′N and 04°00′W to 01°00′E. The samples from November 1962 are from the Fladen and Moray Firth and have been treated separately, as have several single localised hauls (Fig. 3). The numbers of individuals of each species found in the stomachs were raised to the numbers per 10 stomachs, only the stomachs containing food being considered. Owing to the effects of digestion, etc., high accuracy cannot be claimed for the numbers given, but they are adequate for showing the relative importance of different food species. Again, planktonic forms—copepods [*Calanus finmarchicus* (Gunnerus), *Pseudo/Paracalanus*, *Metridia lucens* Boeck], euphausiids [*Meganyctiphanes norvegica* (M. Sars), *Thysanoessa inermis* (Krøyer), *Nyctiphanes couchii* (Bell)], *Parathemisto* sp., *Spiratella retroversa*, appendicularians, *Sagitta* sp., *Tomopteris* sp., larvae of benthic invertebrates and fish eggs and larvae—were found to be of major importance in the food of *T. esmarkii*. In addition cumaceans, mysids, amphipods, isopods, natant decapods (*Crangon allmani* Kinahan, *Spirontocaris* sp.) and polychaetes also occur (Tables II–VII, Figs. 4–9).

Figures 4 to 9 further demonstrate the differences in the stomach contents of juvenile and adult fish. In the southern area in March–April 1961 the stomachs of the juvenile fish contained larger numbers of copepods and larval forms than did the stomachs of the adult fish, while the adults had the greater number of euphausiids, natant decapods and appendicularians (Fig. 4). Similar results were obtained in the same area in March 1962 as regards copepods and larval forms, but euphausiids occurred at similar levels in both size-groups (Fig. 5). Natant decapods were present in the juvenile fish but absent from the adult fish.

A comparison of the data from the northern area in March–April 1961 (Fig. 6) is difficult since the average numbers for juvenile stomachs are based on the data from one trawl haul only, and the absence of certain species cannot be considered significant. Euphausiids are clearly shown, however, as an important food type of the adults. On the Fladen Ground in November 1962 (Fig. 7) the juveniles' stomachs had a greater number of copepods than those of the adult fish, while the latter contained euphausiids and natant decapods—both absent from the juvenile fish. Appendicularians and *Spiratella* were abundant in both sets of stomachs, but *Sagitta* was more abundant by far in the juveniles' stomachs. The data from a number of scattered localities (S62/36, 38, 41, 45) also showed that the stomachs of the juveniles contained greater numbers of copepods (Fig. 8), but euphausiids as a group were equally abundant in both juvenile and adult fish as were also appendicularians. *Sagitta* was found only in the juvenile fish. Figures 7 and 9 show that the results showing high euphausiid content of the juvenile stomachs in November 1962 (Fig. 1) were entirely from two samples from the Moray Firth.

Where juveniles and adults occurred in the same hauls the most consistent difference in stomach contents was that the juveniles had a greater number of copepods per stomach. A less consistent difference was that there tended to be more euphausiids per stomach in the adults.

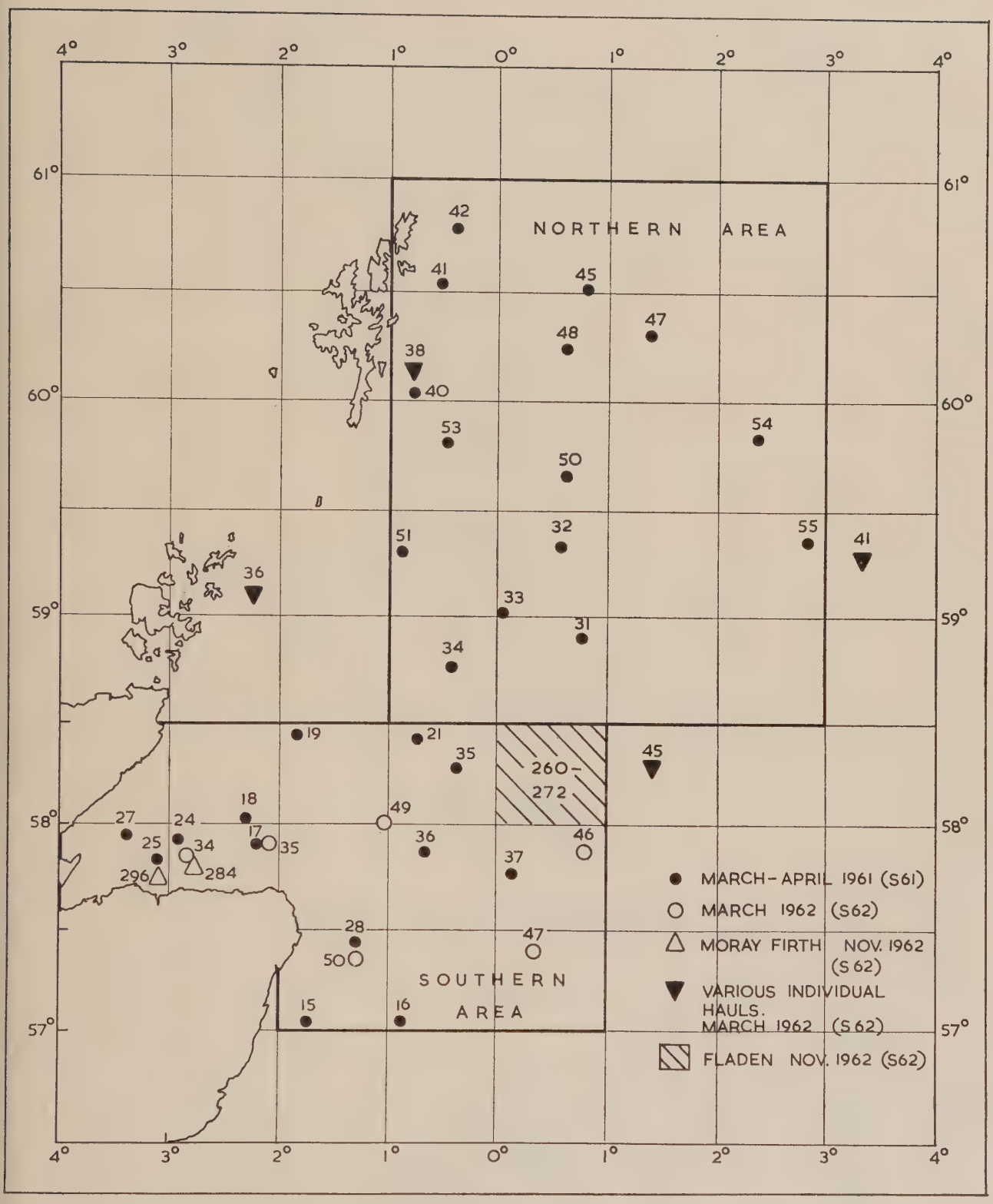

Fig. 3. Sampling areas, 1961 and 1962. Trawl haul numbers shown.

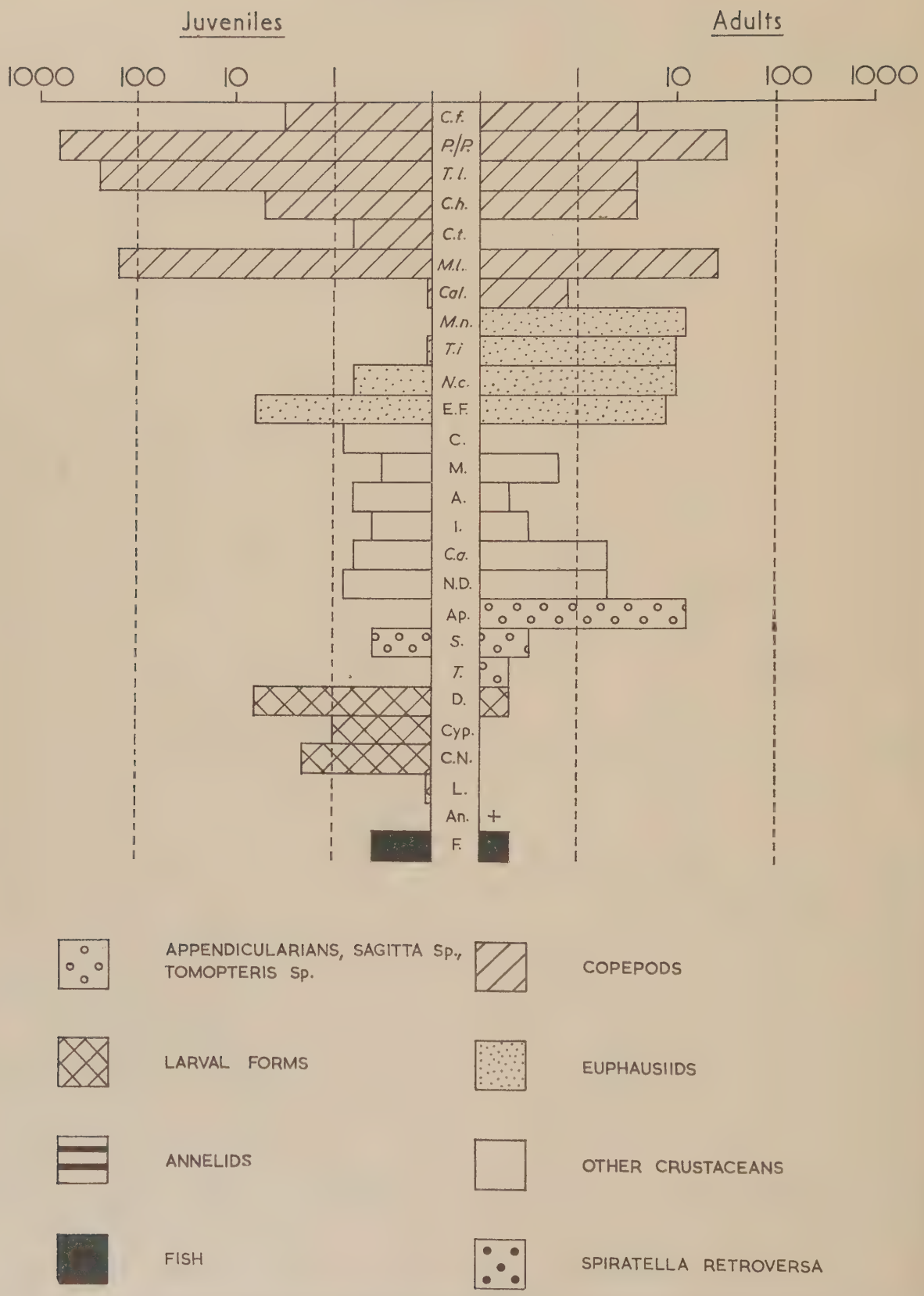

Fig. 4. Food of juvenile and adult fish, southern area 13th March–2nd April 1961. Numbers per 10 stomachs with food (log. scale). Order of species as in Table II.

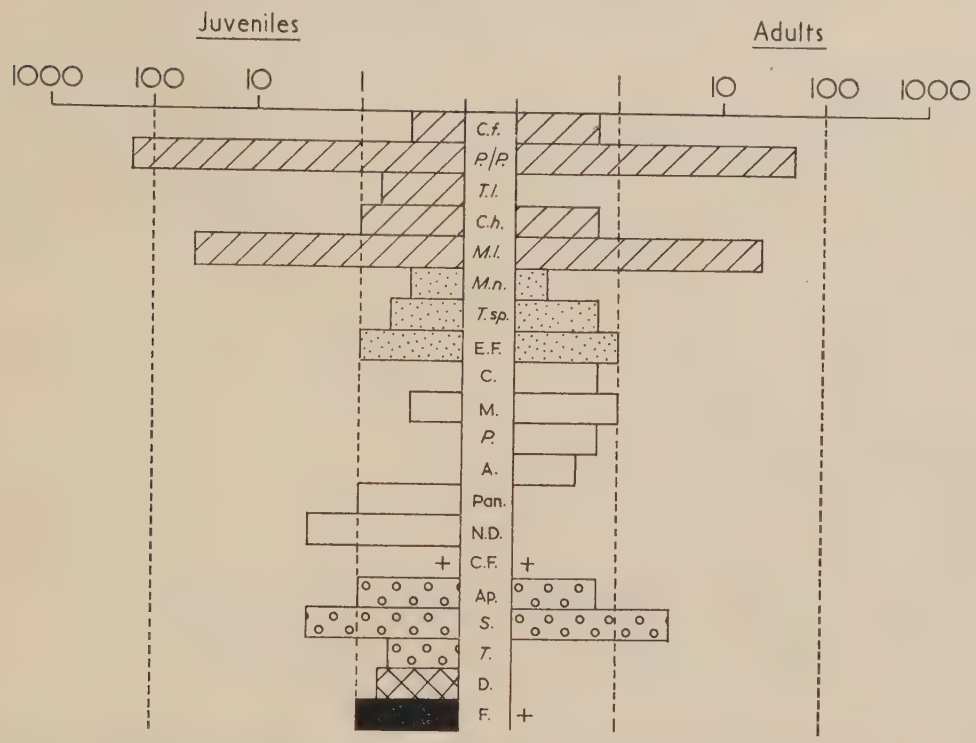

Fig. 5. Food of juvenile and adult fish, southern area, 5th–18th March 1962. Numbers per 10 stomachs with food (log. scale). (Order of species as in Table III and key as in Fig. 4.)

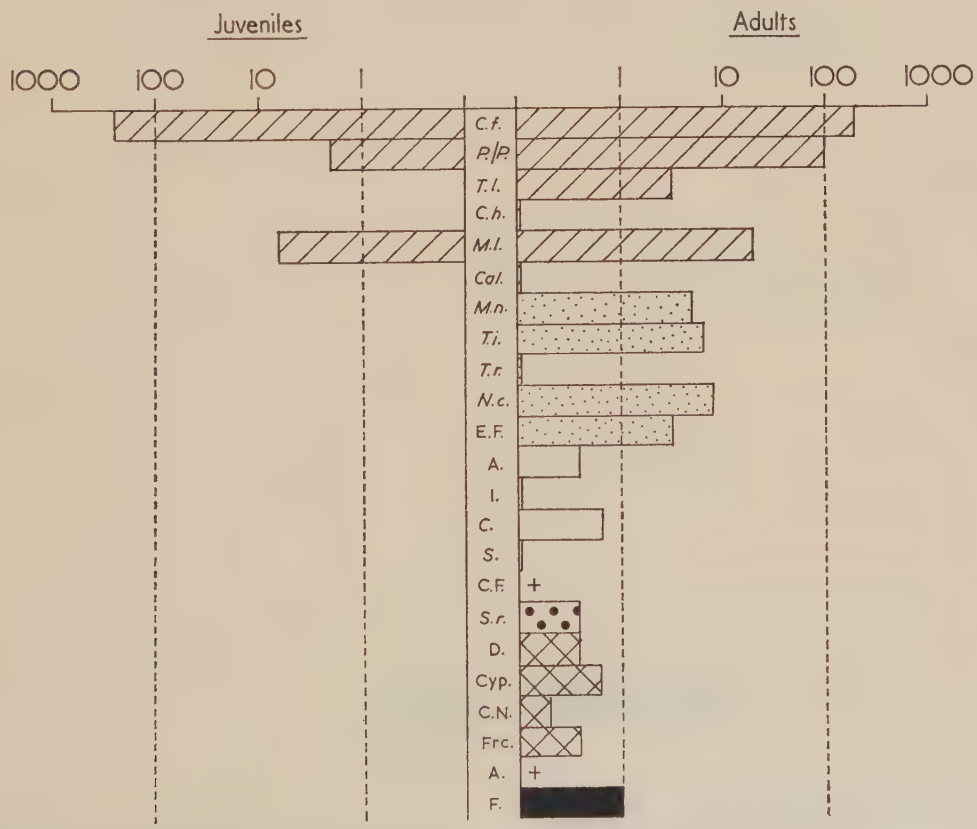

Fig. 6. Food of juvenile and adult fish, northern area, 31st March–15th April 1961. Numbers per 10 stomachs with food (log. scale). (Order of species as in Table IV and key as in Fig. 4.)

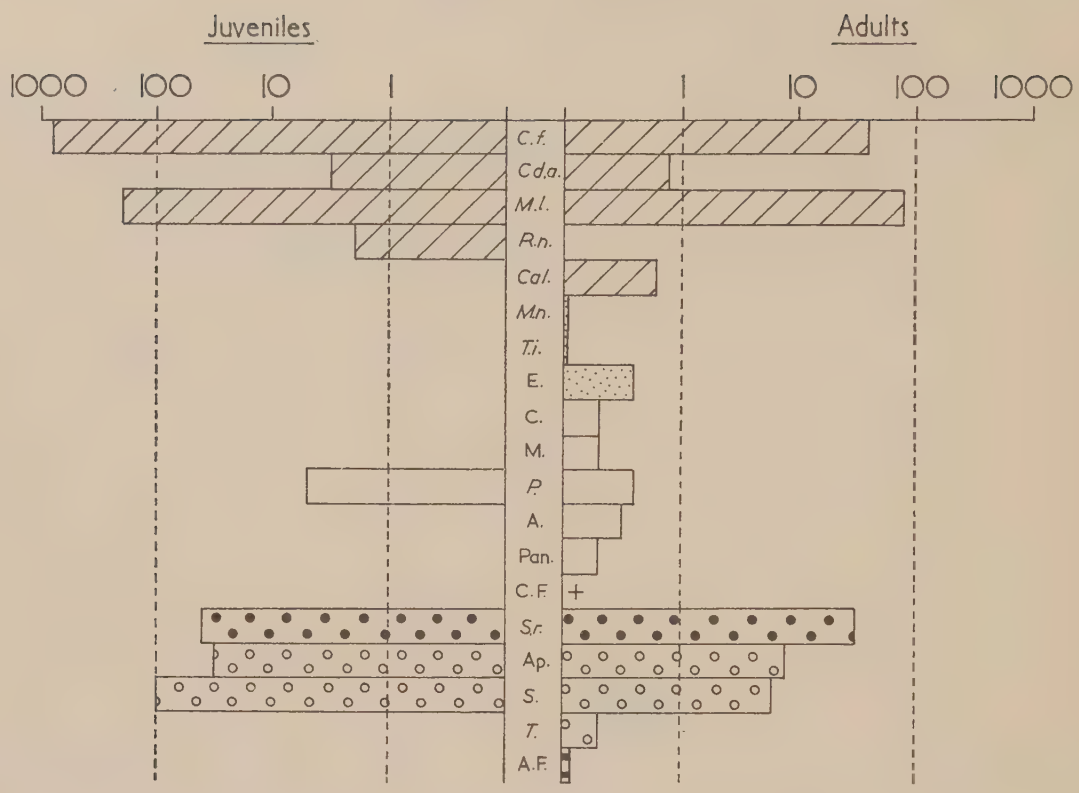

Fig. 7. Food of juvenile and adult fish, Fladen, 12th–17th November 1962. Numbers per 10 stomachs with food (log. scale). (Order of species as in Table V and key as in Fig. 4.)

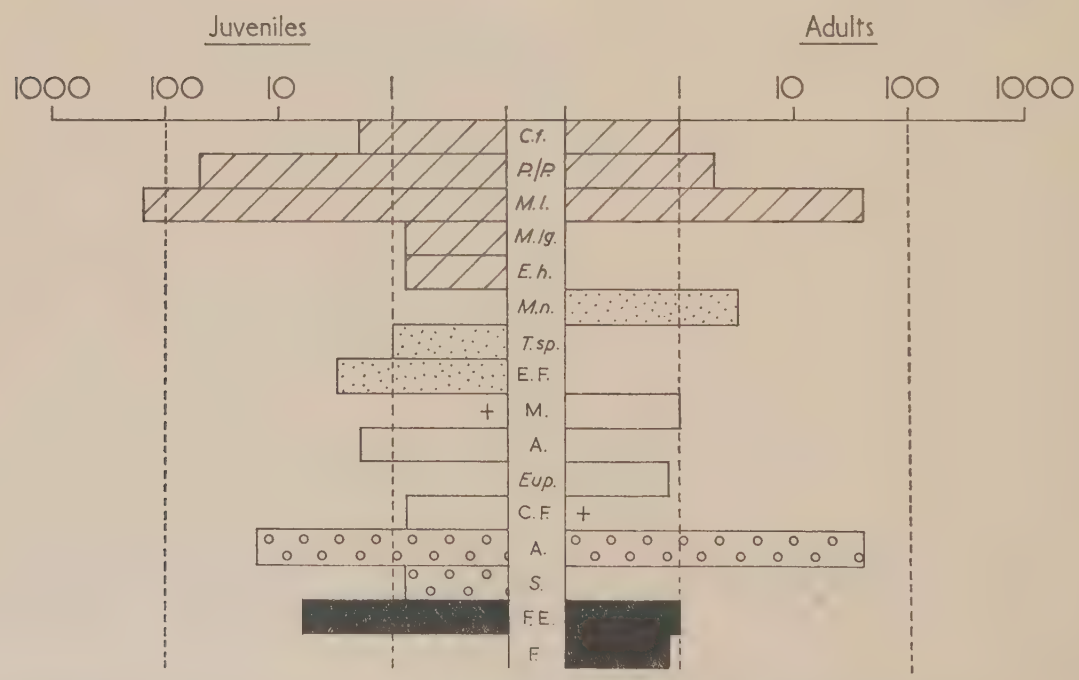

Fig. 8. Food of juvenile and adult fish, various localities (S62/36, 38, 41, 45), 9th–16th March 1962. Numbers per 10 stomachs with food (log. scale). (Order of species as in Table VI and key as in Fig. 4.)

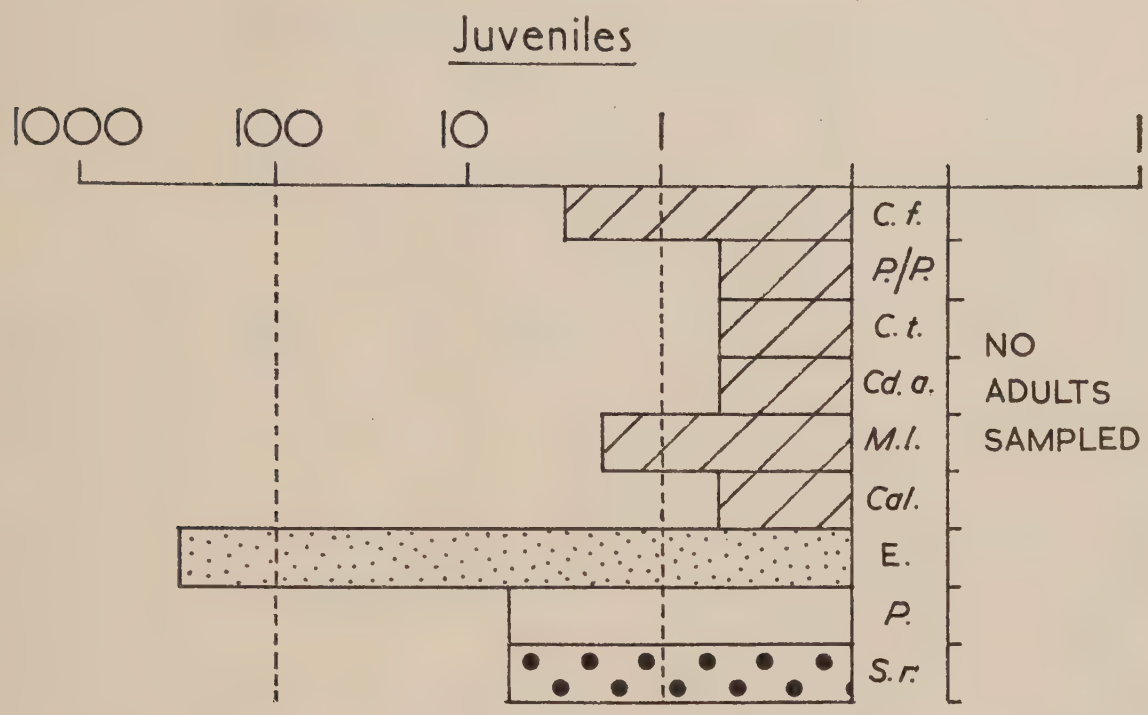

Fig. 9. Food of juvenile fish, Moray Firth, 23rd–26th November 1962. Numbers per 10 stomachs with food (log. scale). (Order of species as in Table VII and key as in Fig. 4.)

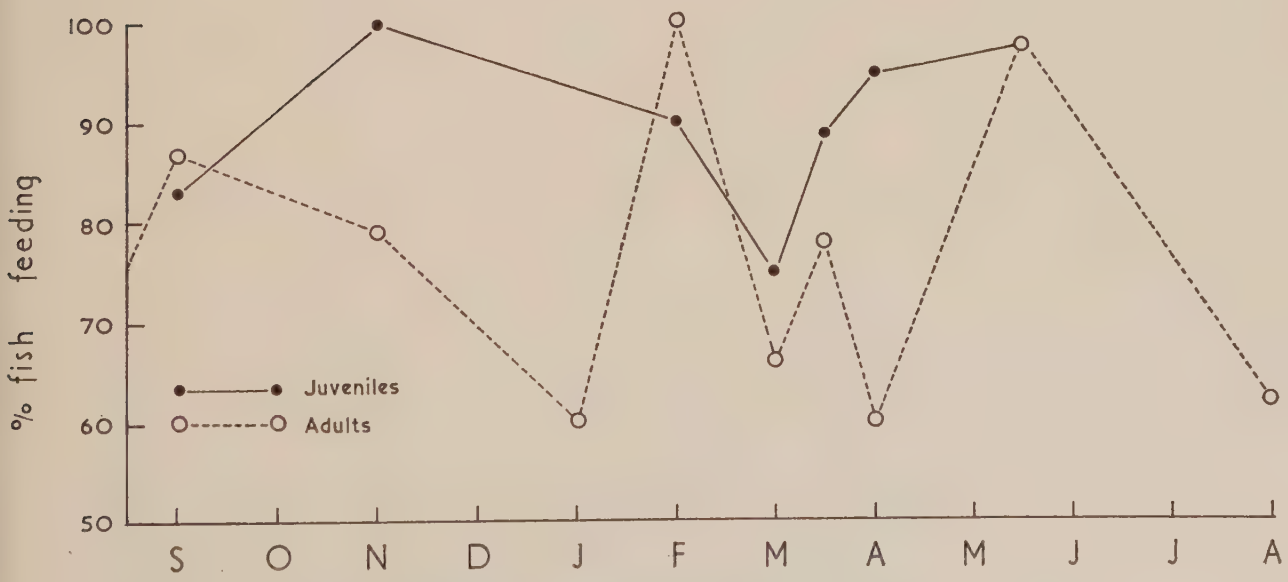

Fig. 10. Seasonal feeding of *T. esmarkii* expressed as the percentage of fish feeding.

TABLE II

T. esmarkii STOMACH CONTENTS; SOUTHERN AREA, 13th MARCH–2nd APRIL 1961

Numbers per 10 stomachs with food

	Juveniles								Adults						
	Trawl haul numbers								Trawl haul numbers						
	S61/16	18	19	24	25	27	37	Average	15	17	21	28	35	36	Average
Calanus finmarchicus (Gunnerus)					1		20	3			2	15		6	4
Pseudo/Paracalanus	3014		426	1			982	632			29	11	48	103	32
Temora longicornis (O. F. Müller)	301	3		22	1066	523	20	276				15		10	4
Centropages hamatus (Lilljeborg)		1		22	2	8		5				9		16	4
C. typicus Krøyer	4							0·6							
Metridia lucens Boeck	24		589				380	142			147	2		7	26
Caligus sp.					1			0·1	2				2	1	0·8
Meganyctiphanes norvegica (M. Sars)									5			49	3	26	14
Thysanoessa inermis (Krøyer)	1							0·1	13		47			6	11
Nyctiphanes couchii (Bell)			5					0·7			62			2	11
Euphausiid fragments			36		11			7			38			17	9
Cumaceans	1					5		0·8							
Mysids		2						0·3	2	1	1				0·7
Amphipods	1					3		0·6		1					0·2
Isopods						3		0·4		2					0·3
Crangon allmani Kinahan		3			2			0·7	5			5			2
Other natant decapods				6				0·8		9	1			1	2
Appendicularians											3			82	14
Sagitta sp.							3	0·4	2						0·3
Tomopteris sp.											1				0·2
Decapod larvae	48							7						1	0·2
Calyptopis							7	1							
Cirripede nauplii				1	10	3		2							
Lamellibranch larvae					1			0·1							
Annelid fragments										+					+
Fish		1	1		1			0·4						1	0·2

TABLE III

T. esmarkii STOMACH CONTENTS; SOUTHERN AREA 5th–18th MARCH 1962

Numbers per 10 stomachs with food

	Juveniles							Adults					
	Trawl haul numbers							Trawl haul numbers					
	S62/34	35	46	47	49	50	Average	34	46	47	49	50	Average
Calanus finmarchicus (Gunnerus)				2			0·3				3		0·6
Pseudo/Paracalanus		684	5	286	23	3	167		3	212	13		46
Temora longicornis (O. F. Müller)		4					0·7						
Centropages hamatus (Lilljeborg)					7		1				3		0·6
Metridia lucens Boeck		16		220	7		40			118	11		26
Meganyctiphanes norvegica (M. Sars)	2						0·3			1			0·2
Thysanoessa sp.						3	0·5				3		0·6
Euphausiid fragments						7	1		5				1
Cumaceans											3		0·6
Mysids	2						0·3			4		2	1
Parathemisto sp.										3			0·6
Amphipods												2	0·4
Pandalids	2	4					1	+					+
Other Natant Decapods	16						3						
Crustacean fragments			+				+		+				+
Appendicularians			5			1	1				3		0·6
Sagitta sp.				19		1	3			7	3	6	3
Tomopteris sp.				3			0·5						
Decapod larvae		2		2			0·7						
Fish	6						1					+	+

TABLE IV

T. esmarkii STOMACH CONTENTS; NORTHERN AREA, 31st MARCH–15th APRIL 1961

Numbers per 10 stomachs with food

	Juveniles	Adults														
	Trawl haul number	Trawl haul numbers														
	S61/54	31	32	33	34	40	41	42	45	47	48	50	51	53	55	Average
Calanus finmarchicus (Gunnerus)	226	10	35	13			2	121	89	30		930	173	2	1693	221
Pseudo/Paracalanus	2	1		610	882	77	2	8	6			3	8		17	115
Temora longicornis (O. F. Müller)										2		15	18	6		3
Centropages hamatus (Lilljeborg)			1					1								0·1
Metridia lucens Boeck	6	2	11	30	147	7	5	18	19	16		6	13	8		20
Caligus sp.							2									0·1
Meganyctiphanes norvegica (M. Sars)		15	+	10	24					16						5
Thysanoessa inermis (Krøyer)				57	1			23	7	15						7
T. raschii (M. Sars)										1						0·1
Nyctiphanes couchii (Bell)								3	4	102					1	8
Euphausiid fragments		12		24	+				6							3
Amphipods				1					4						1	0·4
Isopods								1								0·1
Crangon allmani Kinahan							10									0·7
Spirontocaris sp.					1											0·1
Crustacean fragments											+					+
Spiratella retroversa (Fleming)			1					4				1				0·4
Decapod larvae							2		3							0·4
Calyptopis								1	7							0·6
Cirripede nauplii													3			0·2
Furcilia									1	2			3			0·4
Annelid fragments							+									+
Fish								7	7	1						1·0

TABLE V

T. esmarkii STOMACH CONTENTS; FLADEN, 12th–17th NOVEMBER 1962

Numbers per 10 stomachs with food

	Juveniles				Adults											
	Trawl haul numbers				Trawl haul numbers											
	S62/263	266	270	Average	260	262	263	264	265	266	267	269	270	271	272	Average
Calanus finmarchicus (Gunnerus)	2045	812		952	88	33	217	17	42	13		34	13	4		42
Candacia armata Boeck	5	3		3			3		4	1		1				0·8
Metridia lucens Boeck	320	143	140	201		6	211	66	121	105	2	194	125	20	12	78
Rhincalanus nasutus Giesbrecht	5			2												
Caligus sp.					2			2		1		1	1	1		0·7
Meganyctiphanes norvegica (M. Sars)												1				0·1
Thysanoessa inermis (Krøyer)							1									0·1
Euphausiids					2				2							0·4
Cumaceans										1			1			0·2
Mysids									2							0·2
Parathemisto sp.	15			5		3	2									0·4
Amphipods											2	1				0·3
Pandalids					2											0·2
Crustaceans fragments									+		+					+
Spiratella retroversa (Fleming)		13	95	36	2		1	1		72	70	95	79	16	6	31
Appendicularians	90			30			60	42								9
Sagitta sp.	245	57	5	102	10		41	1	4					8		6
Tomopteris sp.						1	1									0·2
Annelid fragments						1										0·1

TABLE VI

T. esmarkii STOMACH CONTENTS; VARIOUS, 9th–16th MARCH 1962

Numbers per 10 stomachs with food

	Juveniles					Adults				
	Trawl haul numbers					Trawl haul numbers				
	S62/36	38	41	45	Average	36	38	41	45	Average
Calanus finmarchicus (Gunnerus)		3		3	2		5			1
Pseudo/Paracalanus		33		153	46		10			2
Metridia lucens Boeck		630		10	160		160			40
M. longa (Lubbock)		3			0·8					
Euchaeta hebes Giesbrecht		3			0·8					
Meganyctiphanes norvegica (M. Sars)								12		3
Thysanoessa sp.	5				1					
Euphausiid fragments			13		3					
Mysids	+				+	5				1
Amphipods			3	6	2					
Eupagurus sp.									3	0·8
Crustacean fragments		3			0·8	+		+		+
Appendicularians		65			16		160			40
Sagitta sp.			3		0·8					
Fish eggs		25			6		5			1
Fish									3	0·8

TABLE VII

T. esmarkii STOMACH CONTENTS; MORAY FIRTH, 23rd–26th NOVEMBER 1962

Numbers per 10 stomachs with food

	Juveniles		
	Trawl haul numbers		
	S62/284	296	Average
Calanus finmarchicus (Gunnerus)	4	2	3
Pseudo/Paracalanus		1	0·5
Centropages typicus Krøyer		1	0·5
Candacia armata Boeck		1	0·5
Metridia lucens Boeck	2	2	2
Caligus sp.		1	0·5
Euphausiids (*Thysanoessa inermis* (Krøyer) and *Nyctiphanes couchii* (Bell))	323	254	288
Parathemisto sp.	7	7	7
Spiratella retroversa (Fleming)		12	6

VARIATIONS IN FEEDING

Seasonal

The numbers of stomachs containing food have been used as an index of the intensity of feeding at different times of the year (Fig. 10). Apart from a slight drop in March the juveniles show little variation in feeding throughout the year while they are still distinguishable from the adult population. The graph for adult fish, however, suggests that there may be three periods of low feeding intensity, in January, March–April and August, but the points for January and February are based on only 10 observations each. A decline in feeding would be less improbable in March and April, however, since this is the main spawning period of *T. esmarkii*. Correspondingly, what appears to be a peak feeding period in May–June occurs at a time of high zooplankton abundance in the northern North Sea, while the smaller peak in September also coincides with the small peak in zooplankton abundance usually found then (Colebrook and Robinson, 1961).

The average volumes of total food per 1,000 stomachs at different times of the year (considering only stomachs containing food—Table VIII) show the same general trends as those in Figure 10.

TABLE VIII

AVERAGE VOLUME OF FOOD PER 1,000 STOMACHS WITH FOOD (C.C), JUVENILES AND ADULTS, 1960–62

Month	1960		1961		1962		Average	
	Juv.	Adults	Juv.	Adults	Juv.	Adults	Juv.	Adults
March	—	—	—	—	61	59	61	59
March–April	—	—	112	200	—	—	112	200
April	95	57	—	—	—	—	95	57
May	—	—	—	—	—	1,445	—	1,445
May–June	—	98	—	—	—	—	—	98
June	—	—	—	—	—	—	—	—
July	—	—	—	—	—	—	—	—
August	—	41	—	170	—	—	—	106
September	58	192	—	—	—	—	58	192
October	—	—	—	—	—	—	—	—
November	—	—	—	—	177	57	177	57

Diurnal

Most of the samples were collected during the hours of daylight. In November 1962, however, several night hauls were made and Figure 11 shows that the average volume per stomach with food during this survey for both juveniles and adults was highest at about 1400 hours G.M.T. Data from other cruises (Fig. 11) could be interpreted as showing that there was a higher feeding intensity during daylight but it is obviously impossible, owing to the lack of night hauls, to come to any firm conclusion.

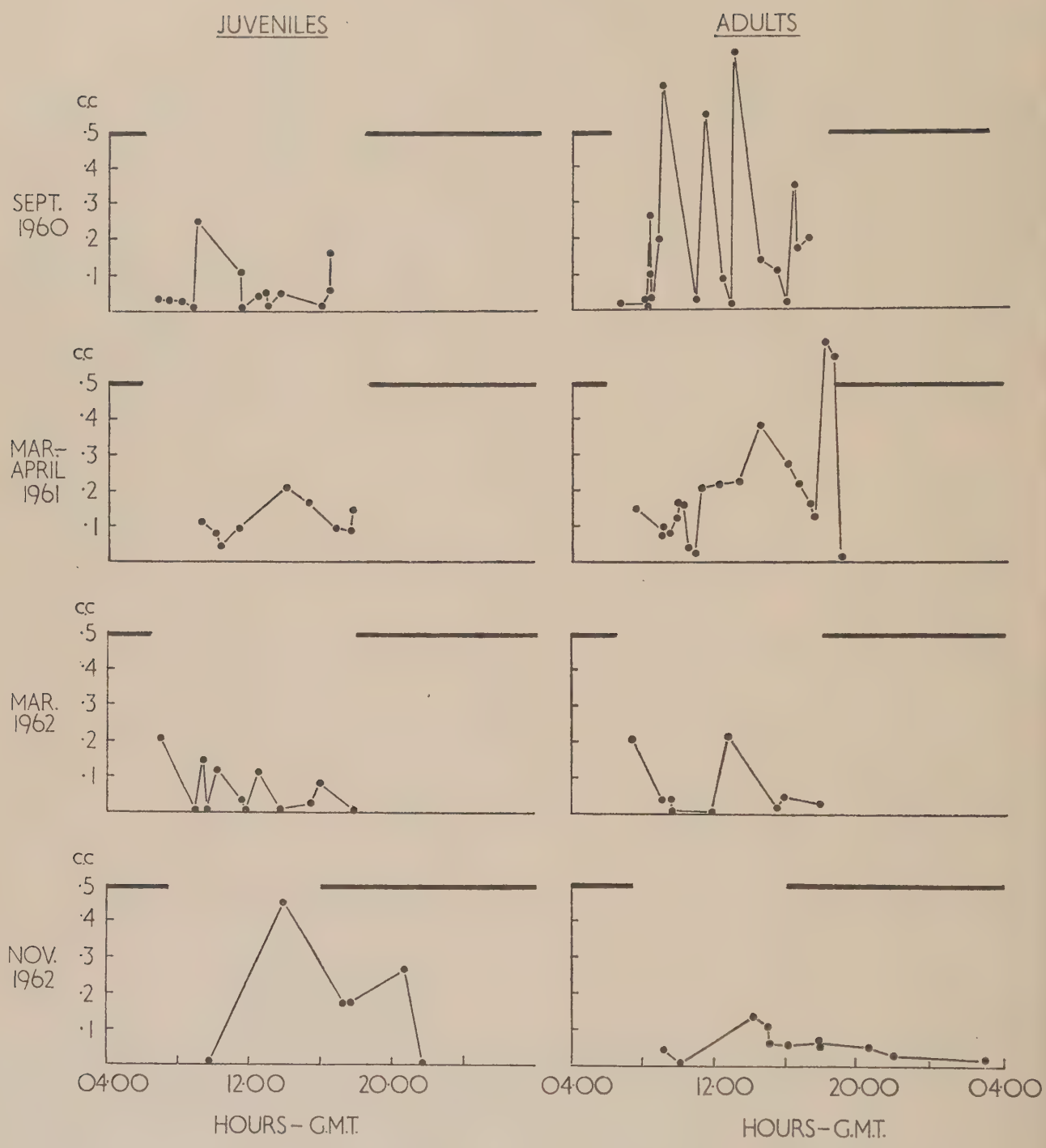

Fig. 11. Diurnal changes in average volume per stomach with food, juveniles and adults. (Hours of darkness indicated.)

RELATIONS BETWEEN THE FOOD OF *T. ESMARKII* AND THE ZOOPLANKTON

For this comparison the food and the planktonic species have been grouped into two categories in three areas investigated; (*a*) "small organisms"—copepods, *Spiratella retroversa,* and *Pneumodermopsis paucidens* Boas—and (*b*) "large organisms"—including euphausiids, *Sagitta* sp., *Tomopteris* sp., appendicularians, etc. This grouping is, of course, arbitrary, and there are large size-ranges within each group. No species in the appropriate categories occurring in the zooplankton samples in numbers less than 1·0 per m^3, 1·0 per 10 m^3 or 1·0 per 100 m^3 (depending on the scale in use) has been included. A few species below these levels of abundance or not recorded from the Gulf III samples were, however, found in the stomachs. These were:

Southern Area 1961	*Centropages typicus* Krøyer (0·3 per 10 stomachs); *Caligus* sp. (0·5); appendicularians (6·5).
Southern Area 1962	*Metridia lucens* (34); *Temora longicornis* (O. F. Müller) (0·4); *Centropages hamatus* (Lilljeborg) (0·9); decapod larvae (0·4).
Northern Area 1961	*Temora longicornis* (2·7); *C. hamatus* (0·1); *Caligus* sp. (0·1); *Meganyctiphanes norvegica* (4·3); *Spiratella retroversa* (0·4).
Fladen 1962	*Candacia armata* Boeck (1·2); *Rhincalanus nasutus* Giesbrecht (0·4); *Caligus* sp. (0·6); *Tomopteris* sp. (0·1).

Apart from a few important exceptions (numbers per 10 stomachs underlined), species present in the zooplankton at densities below these levels are unimportant in the stomachs. Exact counts of invertebrate larvae were unfortunately not obtained for the 1961 Gulf III samples, but they did occur in the stomachs (see Tables II and IV).

The relative abundance of "small organisms" is similar in the zooplankton and in the stomachs, the numerically dominant species in the zooplankton being always the most abundant in the stomachs (Fig. 12). Apart from the Fladen samples in November 1962, however, there is little resemblance between the relative abundance of "larger organisms" in the zooplankton and in the stomachs. It is noteworthy that when reasonable agreement was obtained the "large organisms" were far more abundant in the plankton than on the other occasions. Although *Microcalanus* sp., *Acartia* sp. and especially *Oithona* sp. were fairly abundant in the plankton they were not recorded from the stomachs of *T. esmarkii* during the present investigations. This might be because of their smallness. The data from the northern and southern areas in 1961 suggest selection of euphausiids by *T. esmarkii* but this is not supported by the 1962 data.

In Figure 13 the abundance of *Pseudo/Paracalanus* and *Calanus finmarchicus* in the stomachs is compared with their abundance in the zooplankton. It is clear that an increase of these species in the stomachs was associated with an increase in their abundance in the zooplankton. It should also be noted that there was in general less zooplankton in the areas surveyed during March 1962 (250 mg dry weight/100 m^3) than in the areas surveyed in March–April 1961 (920 mg dry weight/100 m^3). This seems to be reflected in the average volumes per stomach in 1961 and 1962 shown in the first two lines of Table VIII.

The fish examined were all caught with the bottom trawl. As the Gulf III does not effectively sample the extreme bottom layers of plankton a bias might be introduced into the above comparisons. If, however, the fish were only feeding on the bottom layers of plankton more cumaceans and mysids would have been expected in the stomachs.

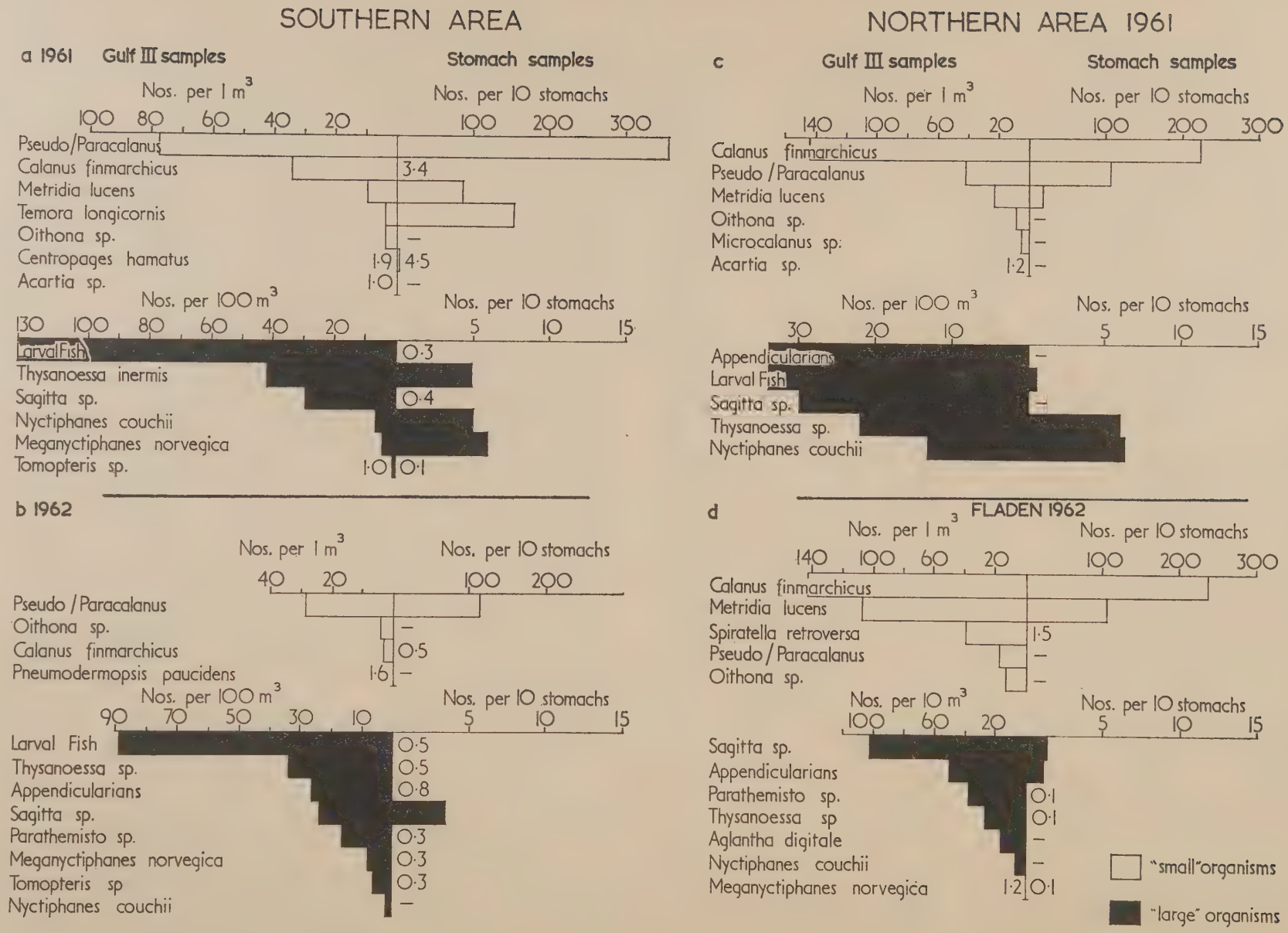

Fig. 12. A comparison of stomach contents with the zooplankton collected at the same position. On the left hand side of each figure the species are arranged in decreasing order of abundance in the plankton samples, expressed as numbers per 1 m³ for the small organisms, and numbers per 100 m³ for the large organisms—with the exception of the Fladen data in November 1962, where the large organisms are expressed as numbers per 10 m³. On the right hand side their corresponding abundance in the stomach samples (juveniles and adults combined) is shown in numbers per 10 stomachs. Unshaded diagrams "small" organisms, shaded diagrams "large" organisms.

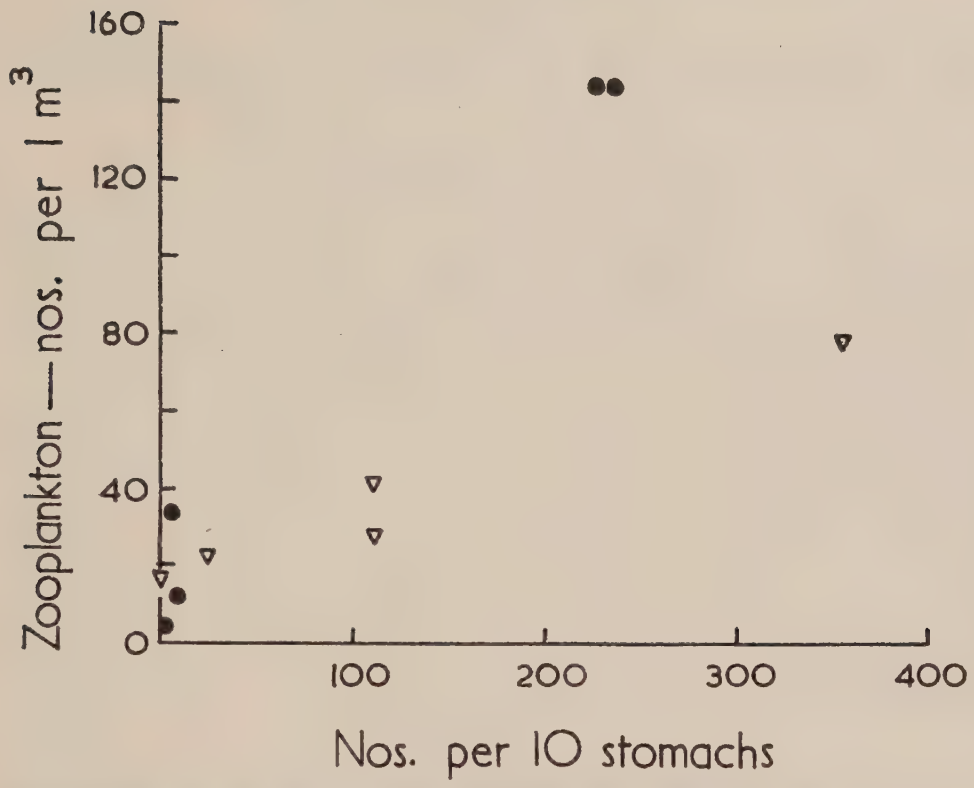

Fig. 13. A comparison of the abundance of *Calanus finmarchicus* and *Pseudo/Paracalanus* in the food of *T. esmarkii* (numbers per 10 stomachs with food) and in the zooplankton (numbers per 1 m³). ● *Calanus finmarchicus*, ▽ *Pseudo/Paracalanus*.

THE FOOD AND FEEDING OF *T. ESMARKII* COMPARED WITH O-GROUP HADDOCK AND WHITING

Records from research trawling surveys in the northern North Sea show that the commonest gadoids in the localities in which *T. esmarkii* occurs are haddock and whiting. It was considered possible that *T. esmarkii* might be a competitor for food with either or both of these closely related species. Stomachs were therefore collected from O-group haddock and whiting less than 20 cm long caught with *T. esmarkii* during five cruises, in September 1960, March–April 1961, August 1961 and November 1962. An analysis of their contents was made in order to determine the extent of the overlap of food types between these species.

Jones (1954) has shown that the food and feeding habits of haddock and whiting differ markedly; it is obvious from the results presented above that *T. esmarkii* is quite unlike haddock in the present samples, which as in Jones' results, were feeding mostly on benthic forms such as polychaetes, echinoderms and molluscs. The haddock, with its ventrally placed mouth, small crushing teeth and sensitive barbel is a typical example of an omnivorous bottom-feeding fish. The whiting, on the other hand, like *T. esmarkii*, feeds on fish and pelagic crustacea. Both species are stream-lined and have a more terminally placed mouth with sharp teeth. The sentive barbel is absent in whiting and reduced in *T. esmarkii*. These two species are characteristic of the active-predator type of fish and thus are suited to a food-source different from that of the haddock.

The food types found in the stomachs of *T. esmarkii* (juveniles and adults combined) and O-group whiting during surveys made in September 1960, March–April 1961 and August 1961 show a substantial overlap (Tables IX, X, XI).

TABLE IX

OCCURRENCE OF FOOD TYPES IN STOMACHS OF *T. esmarkii* AND O-GROUP WHITING, SEPTEMBER 1960

T = *Trisopterus esmarkii* W = Whiting
x = Presence of food type in stomachs

Trawl Number	S60/286		298		300		304		305		306		307		308	
Food Type	T	W	T	W	T	W	T	W	T	W	T	W	T	W	T	W
Thysanoessa inermis (Krøyer)	x				x	x	x	x	x			x	x		x	
Meganyctiphanes norvegica (M. Sars)													x			
Unidentified euphausiids	x	x	x	x		x			x	x	x			x	x	x
Calanus finmarchicus (Gunnerus)	x		x		x		x		x		x				x	
Temora longicornis (O. F. Müller)			x					x								
Metridia lucens Boeck									x							
Candacia sp.				x				x		x						x
Amphipods			x	x	x	x			x	x		x		x	x	x
Crangon sp.	x					x										
Pandalus sp.			x													
Fish remains				x												
Spiratella retroversa (Fleming)			x				x		x	x	x					
Tomopteris sp.							x									
Oikopleura sp.						x		x				x		x		
Sagitta sp.							x		x						x	

TABLE X

OCCURRENCE OF FOOD TYPES IN STOMACHS OF *T. esmarkii* AND O-GROUP WHITING, MARCH–APRIL 1961

T = *Trisopterus esmarkii* W = Whiting
x = Presence of food type in stomachs

Trawl Number	S61/17		21		25		27		31		51	
Food Type	T	W	T	W	T	W	T	W	T	W	T	W
Euphausiids	x	x	x				x		x	x		
Copepods			x		x		x				x	
Amphipods	x	x					x					x
Crangon sp.					x	x						x
Pandalus sp.			x					x		x		
Fish larvae				x								
Fish remains		x			x	x		x				
Decapod larvae				x	x			x			x	
Polychaetes								x		x		x
Sagitta sp.									x			
Squid				x								

TABLE XI

OCCURRENCE OF FOOD TYPES IN STOMACHS OF *T. esmarkii* AND O-GROUP WHITING, AUGUST 1961

T = *Trisopterus esmarkii* W = Whiting
x = Presence of food type in stomachs

Trawl Number	S61/153		167		171		187	
Food Type	T	W	T	W	T	W	T	W
Thysanoessa inermis (Krøyer)	x		x		x	x	x	
Meganyctiphanes norvegica (M. Sars)	x		x		x	x		
Unidentified euphausiids		x	x	x	x	x	x	x
Calanus finmarchicus (Gunnerus)	x	x	x	x	x	x	x	
Metridia sp.	x		x		x	x	x	
Oithona sp.						x		
Caligus sp.						x		
Themisto sp.					x			
Spiratella retroversa (Fleming)	x						x	
Sagitta sp.			x		x	x	x	
Decapod larvae			x	x				
Fish remains		x	x	x		x		x
Ammodytes sp.		x						
Fish Eggs		x						

A more detailed analysis has, however, been made of the relative importance of the different food species in the stomachs of both species from the Fladen in November 1962. These results are shown in Figure 14. The species and groups eaten by *T. esmarkii* and O-group whiting are almost identical but differences are apparent in the relative numbers in the stomachs. For example, there were fewer copepods and more *Meganyctiphanes,* mysids and *Parathemisto* in the O-group whiting stomachs. Decapod larvae and fish, present in the whiting, were absent from *T. esmarkii.* These differences are still apparent when the results for O-group whiting are compared with those for juvenile and adult *T. esmarkii* separately (see Fig. 7).

That two species of fish have the same food species in their stomachs does not necessarily mean they are competing for food as there may be an abundant supply. As already noted in *T. esmarkii*, the numerically dominant food species in the stomachs were those most abundant in the plankton samples. Competition can arise when the prey involved is limited or scarce. Before any assessment of competition could be made it would be necessary to know the population sizes of both prey and predator. In addition the food requirements of the predators and their depth of feeding compared with the availability of the prey are also important. However, in the large concentrations in which *T. esmarkii* are frequently found intra-specific competition is more likely than inter-specific competition.

It is interesting to note the relatively lower average volume of food per stomach with food recorded in *T. esmarkii* (0·156 c.c; range 0·092–0·207 c.c) compared with that in O-group whiting of the same size range from the same hauls (0·365 c.c; range 0·124–0·880 c.c). This is probably associated with their relative growth rates.

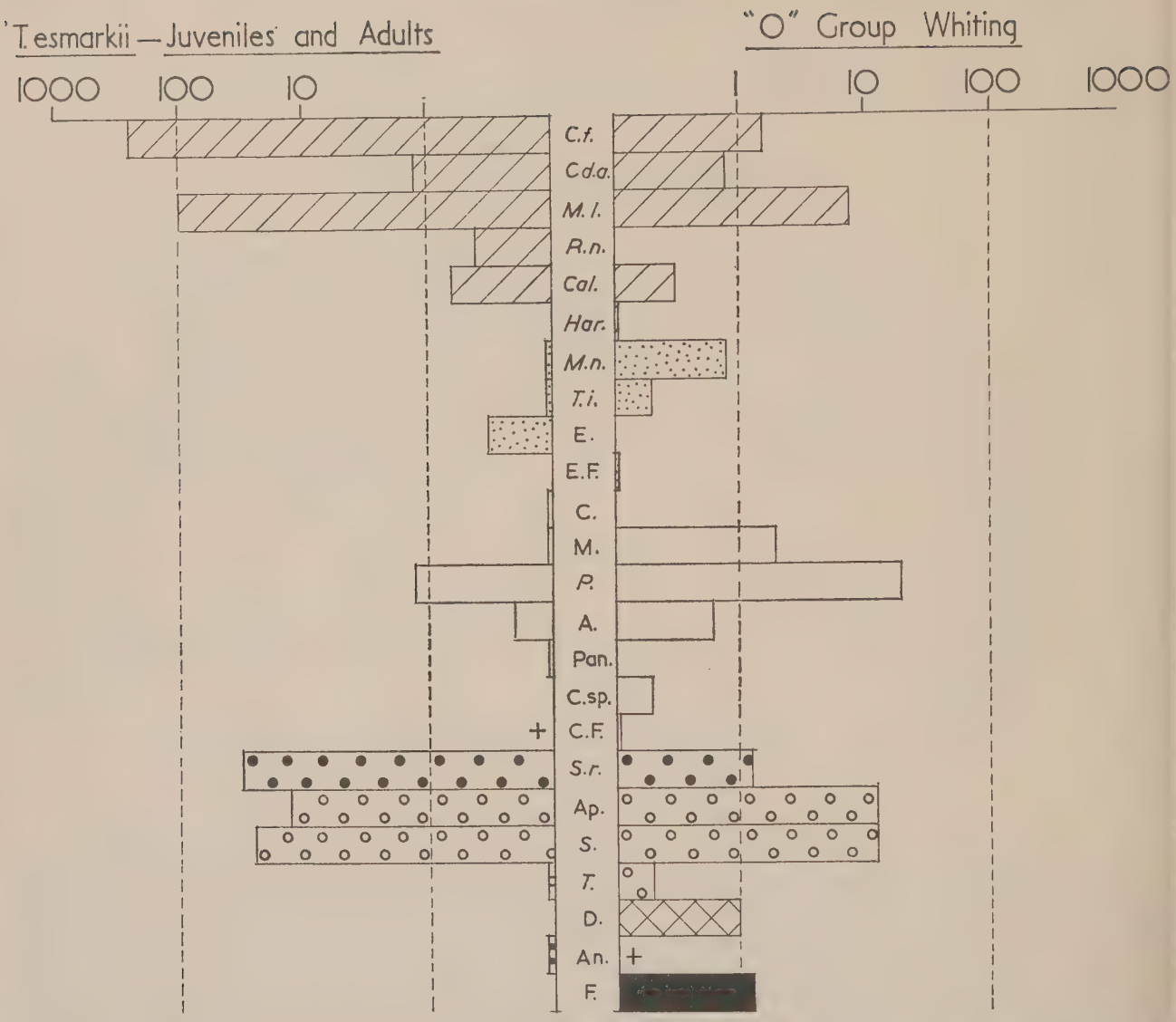

Fig. 14. A comparison of the food of *T. esmarkii* and O-group whiting, Fladen 12th–17th November 1962. Numbers per 10 stomachs with food. *T. esmarkii* food species as in Table V. O-group whiting food species as follows: Har. = harpacticids, E. F. = euphausiid fragments, C.sp. = *Crangon* sp., D = decapod larvae and F = fish. (Key as in Fig. 4.)

T. ESMARKII AS A FOOD SPECIES OF OTHER FISH

T. esmarkii is undoubtedly an important food item in the diet of many larger species of fish but there are few early references to its occurrence in stomachs. Jones (1954), however, shows that in the North Sea it is by far the most important food species of whiting over 21 cm long. Jones reports that early workers on whiting in Scottish waters did not find *T. esmarkii* as a food type since in general their samples were from coastal areas where *T. esmarkii* is not always abundant. Nagabhushanam (1964) also records *T. esmarkii* as an important food item of adult whiting in the deeper water west of the Isle of Man.

Rae (1963) states that it is the most common identifiable fish in the stomachs of megrim from the North Sea and that in this area it is the principal food type of the larger megrim. *T. esmarkii* has also been recorded from the stomachs of cod at certain times of the year in the North Sea (Graham, 1923), and Saemundsson (1949) states that at Iceland it is "of great importance as food for many fishes, particularly cod and ling".

Feeding on *T. esmarkii* has been recorded to a lesser extent in a number of other species. Hickling (1935) working on the food of hake states that he found hake in the Minches between the outer and inner Hebrides "feeding heavily on the pollock whiting (*Gadus esmarkii*)", and Dunn and Holt (1897–9) found specimens in the stomach of a pollack [*Pollachius pollachius* (L.)] off south-west England. Holt (1892), Scott (1910), McIntyre (1953) and Rae (1958) recorded it in the stomachs of halibut from the North Sea, North Atlantic, Faroe and Iceland.

Ritchie (1937) found haddock feeding on *T. esmarkii* only in the autumn off the Shiant Isles and from St Kilda to North Rona. Jones (1954), however, shows the relative insignificance of fish generally in the diet of haddock.

A SUMMARY OF THE POSITION AND IMPORTANCE OF *T. ESMARKII* IN THE FOOD CYCLES OF THE NORTHERN NORTH SEA

T. esmarkii, in common with several other species formerly of no commercial value, particularly sandeels, is now the basis of very important industrial fisheries at certain times of the year by certain countries. Rae (1963) has already commented on the fact that man is now a serious competitor for these species, which are also preyed upon for food by many larger commercial fish. Indeed the short life span and high natural mortality rate of *T. esmarkii* may to some extent be attributable to predation (Fulton, 1901; Raitt, 1960). In addition, an analysis of the stomach contents of O-group whiting has shown that they are often found feeding on the same planktonic species as *T. esmarkii*. Thus the relationship between whiting and *T. esmarkii* may be very complex and the possible effect on the whiting stocks of a decrease in the size of the population of *T. esmarkii* resulting from fishing or natural causes would be very difficult to assess.

SUMMARY

An analysis has been made of the food of *Trisopterus esmarkii* based on an examination of stomach contents. Two size-groups of fish were differentiated; juveniles from 8 to 13 cm, and adults from 14 to 21 cm. Planktonic crustaceans formed the bulk of the diet, copepods and euphausiids being of prime importance. There was evidence to show that the juvenile fish tended to have more copepods in the stomachs than the adults. Other food types occurring included *Sagitta* sp., appendicularians, and natant decapods.

Data on seasonal variations in feeding, although inconclusive, suggested that in the adult fish there may be three periods of low feeding intensity, in January, March–April (the main spawning period) and August. Apart from a slight drop in March, juvenile fish sampled from September to April showed no marked variations in feeding intensity. Both juveniles and adults appeared to have a higher average volume per stomach during the hours of daylight.

A comparison of the stomach contents with the zooplankton in the area, as sampled by the Gulf III showed that the most abundant of the smaller planktonic species were also most frequently represented in the stomachs. An increase in the numbers of *Calanus finmarchicus* and *Pseudo/Paracalanus* in the zooplankton was reflected in an increase in the numbers of these species in the stomachs.

O-group whiting resemble *T. esmarkii* in being principally planktonic feeders with a diet consisting mainly of planktonic crustaceans. Where the stomachs of these two fish were examined from the same trawl haul they frequently had been feeding on the same species. O-group haddock were found to be omnivorous bottom-feeders and quite unlike either of the other two species. This difference in feeding is associated with the morphology and habits of these fish. A review of the literature showed that *T. esmarkii* is an important food of whiting, megrim and cod and to a lesser extent of hake, ling, pollack, halibut and haddock from various areas. The position and importance of *T. esmarkii* in the food cycles of the northern North Sea is briefly discussed.

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